A Study of Homing in the Cotton Mouse,
Peromyscus gossypinus

By

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INTRODUCTION

The term homing may be defined as the return of an animal to a place formerly occupied instead of to other equally probable places (Gerking, 1959). Homing ability and the general problem of spatial orientation have received increasing attention in recent years and have been investigated in widely diverse groups of animals. A considerable number of studies of small terrestrial mammals, principally rodents, have included information on the homing ability of the species concerned (e.g., Aldous, 1937; Allen, 1938; Andersen, 1951; Bowers, 1954; Burt, 1940; Butsch, 1954; Feniuk and Demiashev, 1936; Feniuk and Popova, 1940; Feniuk and Sheikina, 1938; Hacker and Pearson, 1951; Hamilton, 1937, 1939; Harrison, 1958; Hungerford and Wilder, 1941; Johnson, 1926; Kalabukhov and Racoskii, 1933; Keith and Waring, 1956; Kendeigh, 1944; Layne, 1954, 1957; Linsdale, 1946; Löhrl, 1938; McCabe, 1947; Murie and Murie, 1931, 1932; Rawson, 1956; Schleidt, 1951; Schmid, 1936; Seton, 1909; Stickel, 1949; Townsend, 1935). In most of these studies, data on homing have been obtained more or less incidentally to other aspects of the biology of the species being studied. Relatively few investigations, such as those of Rawson (1956), Schleidt (1951), and Stickel (1949), have dealt specifically with homing behavior of small mammals and have involved systematic field and laboratory procedures.

The information presently available on homing in small mammals clearly indicates that there is a general tendency among individuals of many species to return to their home areas when artificially displaced.

There are two major aspects involved in seeking to understand homing behavior in small mammals and other animals as well. The first of these concerns the nature of the motivation to return home. In other words, why should an animal placed in new surroundings similar to those in its home area exhibit a strong inclination to return to its previous quarters? This consideration leads to the question of what factors in the environment of a small mammal constitute "home" to that animal and what is the underlying psychological and physiological basis for the recognition of, and attachment for, the home area. Although much attention has been given to measurements of home range size in mammals, the problems of the psychological implications of the home range to the individual have thus far been largely neglected.

The second aspect involves the actual means utilized by an animal in its efforts to return to the home area. Various hypotheses concerning the means by which small mammals return to their home area have been suggested. Some workers such as Chitty (1937) and Layne (1957) have proposed that animals return from unfamiliar territory through random wandering until and if familiar surroundings are encountered, whereas others, including Burt (1940), Feniuk and Popova (1940), Feniuk and Sheikina (1938), Hamilton (1939), Lindenlaub (1955), Murie and Murie (1931), Neuhaus (1948), and Vogelburg and

Kruger (1951), have postulated the existence of some special sense of direction. The possibility that some animals actually possess a greater range of familiarity with the area around their homes than conventional study techniques indicate has also been suggested as a factor in homing success (Chitty, 1937; Kendeigh, 1944; Murie and Murie, 1931; Stickel, 1949, 1954).

The present paper concerns an investigation of homing behavior in the cotton mouse, Peromyscus gossypinus (LeConte), in northcentral Florida. The study, utilizing approximately 175 individual cotton mice, involved 1) establishment of home range and population estimates as necessary background for other phases, 2) homing displacements at various distances from the capture site to determine the extent of homing ability in natural areas, 3) homing releases in unfamiliar and unnatural habitat of animals from adjacent natural populations at distances similar to those used in natural habitats for the purpose of comparing homing performance, 4) observations on initial orientation with respect to the homesite of animals released in unfamiliar and unnatural habitats, and 5) retention experiments involving the holding of animals in laboratory isolation for extended periods of time to learn the effects of such treatment on subsequent homing performance and home range recognition.

DESCRIPTION OF THE STUDY AREAS

The studies were conducted at four localities in Alachua County; these will be designated as San Felasco, Devil's Millhopper, Ft. Clark, and the golf course.

The San Felasco area was located approximately nine miles northwest of Gainesville. The general region consisted of an extensive mixed hardwood forest, with such trees as laurel oak (*Quercus laurifolia*), magnolia (*Magnolia grandiflora*), holly (*Ilex opaca*), sweetgum (*Liquidambar styraciflua*), and ironwood (*Ostrya virginiana*) being characteristic. This vegetative association, termed mesophytic hammock (Laessle, 1942), has been considered to represent the climax community of much of northern Florida. The ground cover consisted of rather sparce brushy growth, and the litter, duff, leaf-mold, and humus layers were well developed (Figs. 1 and 2). Numerous fallen trees and rotten stumps were present, and a small stream crossed a portion of the study site. The area had been logged, but not in recent years.

The Devil's Millhopper study site, located approximately six miles northwest of Gainesville, consisted of some 90 acres of mixed woodland with a network of trails and footpaths extending throughout the plot. The general aspect of the vegetation was similar to the San Felasco area except for sparser ground cover in the wetter regions and the presence of some drier sections supporting grassy pine

Figure 1. View of San Felasco study area.

Figure 2. General view of type of natural habitat in which studies were conducted.

Figure 1

Figure 2

flatwoods. A large sink about 125 feet in depth was located in the approximate center of the region. The Devil's Millhopper station was bordered on the south by a paved road and pine foatwoods and on the remaining sides by farmland.

The Ft. Clark area was situated about eight miles west of Gainesville, and consisted of approximately 200 acres of mesophytic hammock that was somewhat drier than the San Felasco study site. The area was generally flat and vegetatively relatively uniform throughout. It was bordered by farms, a limestone quarry, and the remnants of a cut-over pine flatwoods. The area was bisected by a sand road 50 to 65 feet in width. The woodland bordering the north side of the road was about 1000 by 5000 feet in extent, while that on the south side of the road was 2500 by 3000 feet.

In addition to P. gossypinus, other small mammals trapped or seen on the study plots in natural areas included the golden mouse (Ochrotomys nuttalli), gray squirrel (Sciurus carolinensis), cotton rat (Sigmodon hispidus), long-nosed shrew (Sorex longirostris), short-tailed shrew (Blarina brevicauda), cottontail (Sylvilagus floridanus), and the flying squirrel (Glaucomys volans). A common associate of P. gossypinus in the San Felasco area was Ochrotomys nuttalli.

The golf course used in the study was located at the western edge of Gainesville. Its over-all dimensions were approximately 2200 by 2200 feet, and it was bordered on the north by a paved highway, on the east by a residential section, and on the south by cultivated lands of the University of Florida Agricultural Experiment Station

(Fig. 3). At the western edge of the golf course was a fringe of woodland bordered by a sand road. A hammock of approximately 40 to 45 acres in extent was situated on the other side of the road. The latter was 30 to 45 feet wide and was subject to frequent traffic during the morning and afternoon but little at night. The fairways of the golf course varied from 100 to 200 feet in width and were kept closely cut during the time the experiments were being conducted (Fig. 4). The fairways were separated by park-like stands of oaks and pines. The grass in these areas was mowed less frequently than on the fairways proper, but was never allowed to exceed more than a foot in height. Although gray squirrels (Sciurus carolinensis) inhabited these stands, there was no evidence that cotton mice occurred there naturally.

Figure 3. Aerial view of the golf course study area.

Figure 4. View of one of the release points on the golf course.

Figure 3

Figure 4

HOME RANGE SIZE AND POPULATION DENSITY

In order to better interpret homing results, background information on the extent of normal movements of individual mice and on population densities in the habitat-types was obtained.

Home Range

Data on home range were obtained at the San Felasco station. An area of approximately 20 acres was gridded with stakes at 100-foot intervals, with a total of 88 trapping stations. Two types of live traps, the Sherman trap and a plywood trap with inside dimensions of 2 1/2 inches x 3 inches x 8 inches, were used in this and other phases of the study. Rolled oats were used exclusively as bait. Trapping specifically for home range data was conducted for a period of 11 nights during the two periods, one of six nights from March 22 to March 28, and the other of five nights from April 4 to April 9, 1959. Additional home range data for this population were accumulated incidental to other phases of the study until July, 1959.

All stations were trapped simultaneously with one trap per station. Mice were identified by a system of toe-clipping. Information recorded at each capture included date, trap station, sex and reproductive status, and escape path and refuge site used when liberated. Traps making captures were rebaited and reset at the same

station but not in the same position as before.

Forty-eight cotton mice (25 males, 20 females, 3 juveniles) were trapped a total of 194 times during the course of the home range study. Four to ten captures were available for each of 25 adults (12 males, 13 females) taken a total of 145 times. Of the remaining 23 animals taken, 12 (1 adult male, 4 subadult males, 1 subadult female, 3 adult females, 3 juveniles) were captured only one time each and 11 (4 subadult males, 4 adult males, 2 subadult females, 1 adult female) were taken two to three times each for a total of 26 captures.

Home ranges were calculated by the inclusive boundary strip method (Stickel, 1954) for the 12 adult males and 13 adult females taken a minimum of four times each.

The mean trap-revealed home range was 1.57 ± .17 acres. This value is comparable to that, 1.87 ± .22 acres, found by McCarley (1959) for P. gossypinus in Texas. The home ranges of 12 males averaged 1.82 ± .36 acres, with extremes of 0.45 and 4.36 acres, while those of 13 females averaged 1.44 ± .19 acres, with extremes of 0.22 and 2.75 acres. Although the difference in home range size between the sexes is not statistically significant, it suggests that males tend to have a larger home range than females. Other studies of this species indicate a similar trend.

Pournelle (1950) reported wandering of up to 2800 feet for a male cotton mouse while females appeared to move much shorter distances, and Pearson (1953) found that females of P. gossypinus generally moved less than 125 feet between release and recapture while males generally moved more than 125 feet. Barrington (1949) has shown that males of

this species sometimes wander more than one mile while females wander about 800 feet between captures. Larger average home range size for males than females has been found for other species of *Peromyscus* (Burt, 1940; Blair, 1940, 1942) and similar data are available for a variety of other small mammals.

Population Densities

The number of mice estimated to be resident on the San Felasco study area was 36 (20 males, 16 females), which is equivalent to 1.6 animals per acre. Only mice with two or more captures were considered as residents, and the density is calculated on the basis of an adjusted sampling area which compensates for the probability of some animals having home ranges extending beyond peripheral traps (Dice, 1952). A rough estimate from live trapping results indicated that population densities were relatively the same at the four study sites.

HOMING EXPERIMENTS

Mice used in homing experiments were removed from the traps in the morning and maintained in the laboratory until the time of liberation at night, thus eliminating at least some of the supposed effects, such as increased predation, of releasing nocturnal animals during the day. The mice were always conveyed to and from the study area and laboratory in numbered traps placed in a large container. The movements involved in transporting them over the study area and in the car are considered to have prevented the animals from utilizing kinesthetic cues in subsequent homing tests. Great care was taken to reset traps in the same place each time in an attempt to increase the probability of recapturing an animal upon its return.

Homing experiments were carried out at all four study areas. Since the methods of study differed somewhat in each of these, the results of the experiments in each area are treated separately below.

San Felasco

Following completion of home range studies, homing experiments were conducted on the trapping grid at this station. Individuals were displaced at relatively short distances beyond the limits of their known home ranges. A displacement of 300 feet was approximately equal to the diameter of the average home range. Animals were recorded as

having successfully homed if they were recovered at any station within their calculated home range. Eighteen mice were trapped and displaced during an 18-day interval of irregular trapping. All trap stations were activated during each trapping period. Animals returning from their first release were often released in another direction and at a different distance. Thus, 5 mice were liberated one time, 6 mice were liberated two times, 1 mouse was liberated three times, 4 mice were liberated four times and 2 mice were released five times.

Initial releases were made as follows: 2 males and 1 female at 100 feet, 1 male and 1 female at 150 feet, 1 male and 2 females at 200 feet, 1 male and 1 female at 300 feet, 1 female at 400 feet, 2 females at 500 feet, 2 females at 600 feet, 1 male at 800 feet, and 1 male and 1 female at 900 feet.

Of the 7 males and 11 females displaced, all of the males and 10 of the females successfully homed. A male released at 300 feet was recovered on one occasion one-half the distance to its home range before it was recaptured in its home area. The female that was not recovered was an adult released at 600 feet.

Subsequent liberations of successfully homing animals included 19 releases of females as follows: 2 at 100 feet, 1 at 150 feet, 1 at 200 feet, 2 at 250 feet, 3 at 300 feet, 1 at 350 feet, 2 at 400 feet, 2 at 500 feet, 1 at 550 feet, 2 at 600 feet, 1 at 750 feet, and 1 at 800 feet. In a series of 9 males, 2 were released at 200 feet, 1 at 250 feet, 2 at 300 feet, 1 at 500 feet, 2 at 600 feet, and 1 at 700 feet. Recoveries were made in the case of all males and 18 of the 19

female releases. The female not retaken had been released a second time at a distance of 500 feet in the opposite direction from the first liberation at 600 feet.

The trapping schedule used at San Felasco was such that traps were not always available until several nights following releases. Therefore, it is not possible to present a detailed analysis of the times required for homing at this station. However, the results do indicate that at the distances involved, the mice were generally successful in returning to their home ranges in a short period of time.

It is of interest to note that although in many cases released mice had to travel through a portion of the grid of traps to reach their respective home ranges, only one individual was taken in a trap beyond the boundaries of its previously calculated home region.

Devil's Millhopper

Homing experiments in this area were conducted using 30 trapping stations spaced 20 paces apart in an L-shaped trap line. Two traps were set at each station. Single displacements of 8 males and 9 females were made at distances ranging from 500 to 2000 feet from the place of capture. The releases were made during a trapping period of six consecutive nights in March, 1959, and traps were available for recapture on the night of liberation. Mice were considered to have successfully homed if they were retaken at the original site of capture or in either of the adjacent stations. The 17 displacements were made as follows: 2 males and 2 females at 500 feet, 2 males and 2 females

at 1000 feet, 2 males and 2 females at 1500 feet, and 2 males and 3 females at 2000 feet. Of these mice, 7 males and 6 females homed. Those individuals not recaptured on four nights after liberation included a male released at 1000 feet and a female released at 1500 feet. Two females displaced at 2000 feet were not recovered in five nights of trapping.

The mice that were recovered provide some information on the time and distance relationship in homing. Two males released at 500 and 1000 feet and 3 females released at 500 (2) and 1000 feet were recovered on the night of release. Three males released at 500, 1500, and 2000 feet were retaken on the second night following liberation, while 2 males released at 1000 and 2000 feet and 2 females released at 1000 and 1500 feet were retaken on the third night. A single female displaced 2000 feet was recovered on the fifth night following liberation.

The results of these homing experiments suggest, as has been found in similar studies on other species of small mammals, that homing success decreases as the displacement distance is increased and that there is a general correlation between displacement distance and the time taken to return. A longer time was often necessary to capture animals released at greater distances for the first time. Also, males appeared to be more successful than females in homing from the greater distances.

Ft. Clark

At this study area, homing tests were performed with 12 males and 7 females during April, May, and June, 1959. Two trapping periods were used, each of six consecutive nights. Ten trapping stations were established. Five were located on each side of the sand road about 50 feet within the woodland at intervals of approximately 100 feet. Three traps, spaced 10 to 15 feet apart, were used at each station. Release distances ranged from 400 to 2500 feet from the site of original capture, and mice were considered to have homed only if they returned to any of the three traps at the station of original capture. Successfully homing mice were liberated a number of times usually at another distance and a different direction from that of their first release.

Ten mice were liberated 1 time, 2 mice were liberated two times, 4 mice were liberated three times, 2 mice were displaced four times, and 1 mouse was released five times. The numbers, sexes, and distances involved in the initial releases of the 19 animals included 2 males and 2 females at 500 feet, 1 female at 800 feet, 1 male at 900 feet, 1 male and 1 female at 950 feet, 3 males at 1050 feet, 1 male at 1150 feet, 1 female at 2100 feet, 4 males and 2 females at 2500 feet.

Nine males and 5 females were recovered at the station where first captured, even though many of the displacements were made at a point that made it likely that the mice would encounter traps at several stations if they were to use the direct route in returning to their home-sites. Those mice not recovered included a male and a female displaced

2500 feet, with traps available for three nights for the male and four nights for the female. Two other males released at 1050 and 2500 feet and a female displaced 2500 feet were not retaken during five nights of trapping.

Two males released at 500 and 1150 feet and 2 females liberated at 950 and 2100 feet were retaken on the first night of liberation. Four males released at 500, 900, 950, and 2500 feet, and 2 females released at 500 feet were recovered on the second night. Two males displaced at 1050 and 2500 feet and 1 female liberated at 800 feet were recovered on the third night, and 1 male was retaken from 1050 feet on the fourth night following liberation.

It is of interest to note that 6 of the 19 mice were displaced in the woodland on the opposite side of the road from which they were captured and that 3 of these animals were recovered. Two of these individuals, a male and female, had been displaced at 950 feet and the third, a male, had been released at 2500 feet. Those mice not retaken after removal to the opposite side of the road included 2 females liberated at 2500 feet and 1 male released at 1050 feet.

Subsequent releases of successfully homing animals included six releases of females. Single animals were released at 400, 500, 800, 900, 1150, and 2000 feet. Fourteen releases of males were made as follows: 2 at 450 feet, 1 at 550 feet, 1 at 700 feet, 2 at 850 feet, 1 at 900 feet, 3 at 1200 feet, 1 at 1450 feet, 1 at 1850 feet, 1 at 2000 feet, and 1 at 2500 feet.

Ten mice retaken on the night of liberation included 9 males displaced at 450 (2), 700, 850 (2), 900, 1200, 1450, and 2000 feet and 1

female released at 400 feet. A female liberated at 2000 feet returned on the second night, and a male liberated at 1200 feet returned on the third night. Both animals had been liberated twice before. One male released for the second time at 550 feet was not retaken during the night of release but was recovered 41 days later, on the first night that traps were again available. A female on its second release, at 1150 feet, was not recaptured during the three nights of trapping following liberation but was retaken 46 days later, on the fourth night of a new trapping period. The following animals did not return: 1 male liberated at 2500 feet on its fourth release and a female displaced 800 feet on its second release, while traps were available for two nights. One male liberated at 1200 feet on its third release, 1 male liberated at 1850 feet on its fifth release, and 1 female liberated at 900 feet on its third release were not recovered during three nights of trapping. One female liberated at 500 feet on its second release was not retaken during four nights of trapping.

Nine of the mice released more than one time were taken to the woodland on the opposite side of the road from which they were captured. Six of these, 5 males released at 550, 800, 900, 1200, and 1450 feet and 1 female released at 800 feet, were retaken at their homesites and therefore had to traverse the sand road in returning. The 3 mice not retaken included a male and 2 females liberated at 1200, 500, and 900 feet respectively. Apparently the road did not constitute a strong barrier to homing.

No obvious relationship between time taken to return and release

distance is evident in the data from this area. Four of 19 (21%) mice used in initial releases and 10 of 20 (50%) used in subsequent releases were recaptured on the night of liberation. This suggests, therefore, that homing performance of animals liberated away from home subsequent to the first successful homing trip tends to improve, even though the distances and directions of successive releases are varied.

<u>Summary of Experiments in Natural Habitat</u>

Of 54 mice (27 males, 27 females) displaced for the first time at distances ranging from 100 to 2500 feet, 44 animals (81%) were considered to have homed. Eighty-five percent (23) of the males and 78 percent (21) of the females returned. Every individual of both sexes homed from distances up to 500 feet. At distances from 600 to 2500 feet, 14 of 18 males (78%) and 9 of 15 females (60%) were retaken, indicating that males are more successful than females in homing from the greater distances. A grand total of 101 releases (51 for males, 50 for females), including initial and repeated releases of homing animals, was made at distances varying from 100 to 2500 feet and homing was recorded for 83 percent of the releases. Eighty-six percent of male releases and 80 percent of the female releases resulted in homing. Of the releases ranging from 100 to 500 feet, all of the males (17) and 92 percent of the females (25 of 27) returned. Of the releases ranging from 550 to 2500 feet (34 male releases, 23 female releases) 79 percent (27) of those of males and 65 percent (15) of those of females returned home.

The results of the homing experiments in natural habitats indicate

that homing success in the cotton mouse is inversely proportional to distance at which released. There is a further indication that males and females home with equal success at shorter distances (< 500 feet), while males have a greater probability than females of homing as release distances are increased. The data further suggest, although the relationship is not clear-cut, that, for the range of distances utilized, homing from the initial release is more rapid at the shorter distances. Homing success also appears to improve at both short and long distances with repetitive liberations, even though these are not made at previous release points.

Similar results have been obtained in other studies. For example, Murie and Murie (1931) recorded 87.5 percent return from displacements up to 900 feet and only 30.6 percent from 1050 to 3900 feet for *P. maniculatus*, if only those animals released away from home for the first time are considered. Harrison (1958) working with *Rattus*, reported 83 percent recovery from 1650 feet and 38 percent recovery from rats liberated at 2640 feet. Hacker and Pearson (1951) have noted a similar trend in homing ability in *Apodemus sylvaticus*, and Burt (1940) using *P. leucopus* showed that 76 percent of the mice were retaken from displacements of 30 to 465 feet while only 33.3 percent of those liberated from 480 to 1095 feet were recovered.

Golf Course

From March to early September, 1959, homing studies were carried on at the golf course, utilizing mice from adjacent natural habitats.

The object of this phase of the study was to obtain data on homing success from what could be considered totally unfamiliar and unnatural habitat for comparison with those obtained in natural habitats. Trapping was conducted in two wooded plots located in the northwest and southwest corners of the golf course and in the hammock west of the sand road. Sixteen trapping stations were established in the northwest corner where the habitat suitable for cotton mice was limited to approximately one-half acre. At the southwest corner 12 trapping stations were used, the area being somewhat smaller than that in the northwest corner. The same stations were used throughout the study. No particular arrangement or spacing of traps was utilized, and mice were considered to have successfully homed if retaken at any of the traps in which they were originally captured, since the areas were small enough to correspond with the home range of the animals. In the large woodland, 40 stations were arranged in a U-shaped pattern with about 30 yards between stations. Mice were recorded as successfully homing if retaken at the original site of capture or in either of the adjacent trapping stations. Single traps were used at the stations in the study plots at the edge of the golf course and two traps set within 10 to 20 feet of each other were used in the hammock west of the road.

Animals captured in the peripheral areas were released at selected sites on the fairways. No release site had trees nearer than 100 feet. Some of the successfully homing animals were released a number of times from the same release point to learn the effect of repetitive liberations in unnatural habitats on homing performance. In a very few

instances, the release site was shifted between successive releases.

Forty-seven mice were initially released on the golf course at distances ranging from 1000 to 2700 feet from the site of capture in the adjacent woodlands. In all cases, traps were available for recapture for three nights, including the night of release, and in many instandes for as long as 14 nights after each series of releases. Three males, 2 females, and 1 juvenile were released at 1000 feet, 1 male and 1 female at 1700 feet, 1 male and 2 females at 1800 feet, 4 males and 1 female at 1900 feet, 3 males and 3 females at 2200 feet, and 18 males and 7 females at 2700 feet. Fifteen of these animals (10 males, 5 females) were subsequently recovered at their homesites. The 10 males retaken had been displaced at 1000 (3), 1700 (1), 1800 (1), 1900 (1), and 2700 feet (4). Five females homed from 1000 (2), 1700 (1), 1800 (1), and 2700 feet (1). All of the animals that returned from 1900 feet or more had to cross the sand road in order to reach their home areas.

No animals were recovered on the night of release. A female released at 1000 feet, 1 female and 1 male liberated at 1700 feet, 1 female released at 1800 feet, and 2 males released at 2700 feet had returned by the second night.

Three males and a female that homed from 1000 feet were displaced at a time when traps were available for recapture on four consecutive nights, yet none of these animals was retaken during this period. However, the males were captured on the first night of the next trapping period, 35 nights after displacement, and the female was taken on the third night of the same trapping period, 37 nights after liberation.

The male retaken from 1800 feet had been liberated when traps were available for recapture for seven consecutive nights, but he was not retaken until the fourth night of a trapping period 17 nights after liberation. The male retaken from 1900 feet was recovered on the fourth night following liberation.

One male released at 2700 feet was not recaptured during the six nights that traps were set following liberation but was recovered 26 nights after displacement on the first night that traps were again available. Another male that homed from the same distance was not recovered during the four consecutive nights that traps were available following displacement, but was recaptured on the third night after liberation at a point 2500 feet north of its original site of capture. This individual was later recovered in its home area on the first night of a trapping period, 40 nights after the original displacement. Traps had been available to this animal a total of 14 nights between the time of liberation and subsequent recapture in its home area.

The only female retaken from 2700 feet was not recovered during the six nights that traps were activated following liberation. She was retaken on the first night of a trapping period 40 nights after displacement, although the traps were available for a total of 13 nights in the interval between the time of release and recovery.

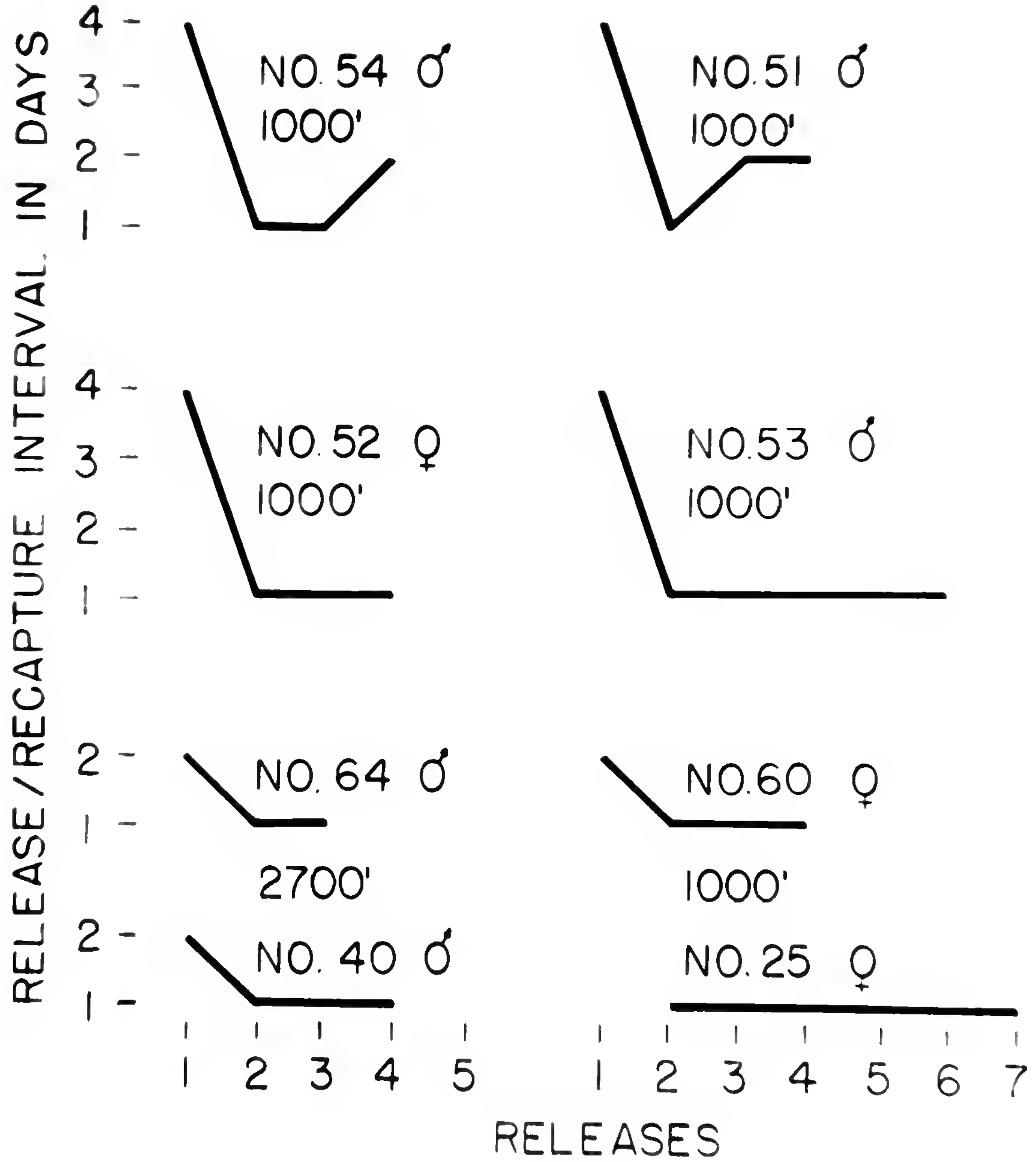
Several animals were recaptured at points other than their home areas. Two males and a female released at 2700 feet and a male released at 2200 feet northeast of their homesites were trapped approximately 2500 feet north of the homesite. The single juvenile released

1000 feet west of its home area was recaptured 2200 feet south of the site of original capture, and a female displaced 2200 feet northeast of its homesite was recovered 400 feet east of the original capture site.

Seven of the 15 animals recaptured in the home area were liberated a number of times from the same release point. The results of these tests clearly indicate that the animals home more rapidly from the same release site following the first return. This trend is illustrated in Fig. 5, where the length of time taken by the mice to return from successive releases from the same point over distances of 1000 to 2700 feet is shown graphically. In most instances time intervals were measured in nights, since traps were checked only on the morning following release. However, on one occasion periodic checks were made after release and a close approximation to the actual time taken to return from 1000feet was obtained for 3 animals that had homed from the same point previously. A female, No. 60, released for the third time, returned in less than three hours. Another female, No. 52, and a male, No. 53, which had been released for the third and fifth times, respectively, were back in the traps within two hours.

Summarizing these results, of 6 mice (3 males, 2 females, 1 juvenile) released at 1000 feet, only the juvenile did not return to its homesite. Ten mice (6 males, 4 females) were liberated at 1650 to 2150 feet and 3 males and 2 females were recaptured. Four males and 1 female, of 31 animals (21 males, 10 females) liberated at from 2200 to 2700 feet, were recovered. No recaptures were recorded on the night

Figure 5. Effect of multiple releases from the same point on time of return in golf course experiments.



RELEASE/RECAPTURE INTERVAL IN DAYS
NO. 54 ♂
1000'
NO. 51 ♂
1000'
NO. 52 ♀
1000'
NO. 53 ♂
1000'
NO. 64 ♂
NO. 60 ♀
2700'
1000'
NO. 40 ♂
NO. 25 ♀
RELEASES

Figure 5

of release. Six of the 15 animals that homed returned by the second night following liberation, the other 9 mice taking an excessive amount of time for recovery. Of the total number of adult mice released (46) on the golf course at 1000 to 2700 feet, 5 of 16 females (31%) and 10 of 30 males (33%) returned to their home areas. Successfully homing animals released repetitively from the same point at distances ranging from 1000 to 2700 feet from the homesite clearly improved their homing performance.

The data from homing releases made on the golf course provide a basis for comparison with those in natural areas. It should be pointed out that the highway, residential areas, and cultivated lands at the northern, eastern, and southern borders of the golf course could have acted as barriers to the animals and may have directed their movements to some extent. The sand road bordering the west side of the golf course may to some extent have been a barrier to homing but the recovery of some individuals from the mesophytic woodland on the other side of the road indicates that it probably did not hamper movements excessively. The results of the Ft. Clark experiment further support this contention.

The shortest distance at which releases were made on the golf course was 1000 feet. The homing success at this distance was closely similar to that in natural habitats (Fig. 6). However, nearly all animals released at this distance in natural habitats were recovered by the second night following liberation. In the case of the golf course releases only 1 animal returned by the second night of trapping.

Figure 6. Comparative homing success of mice in natural and unnatural habitats.

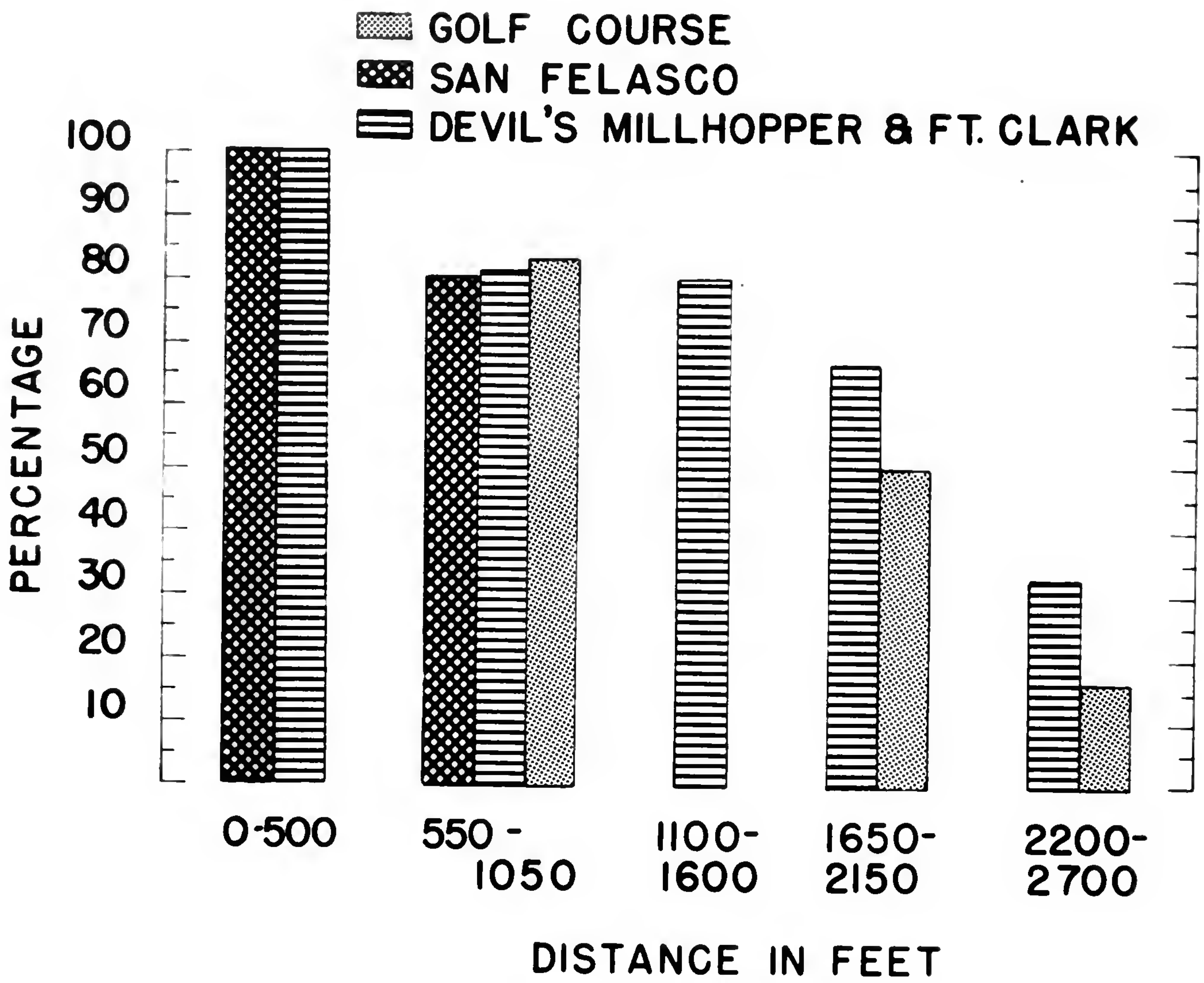

GOLF COURSE
SAN FELASCO
DEVIL'S MILLHOPPER & FT. CLARK
PERCENTAGE
100
90
80
70
60
50
40
30
20
10
0-500
550 - 1050
1100- 1600
1650- 2150
2200- 2700
DISTANCE IN FEET

Figure 6

Other animals released at 1000 feet took more than four nights to return.

Three of the 10 mice liberated at 1650 to 2150 feet on the golf course returned by the second night following release. All of these mice were residents of the southwest corner of the golf course which was near rows of pig pens on the Agricultural Experiment Station lands. The loud and frequent clanging of the feeding trough doors by the pigs may have provided an auditory cue for these mice which might explain their relatively rapid return. Two other mice homing from 1650 and 2150 feet took an excessive amount of time to be recaptured. Four of the 6 mice released at 1650 to 2150 feet in natural areas were retaken, 1 on the night of liberation, 1 on the second night, 1 on the third night, and 1 on the fifth night of trapping. In comparing homing success in natural habitat to homing success from the golf course, no clear-cut difference was found at release distances of 1650 to 2150 feet although there is a tendency for mice to return more rapidly in natural areas.

In the group of mice released from 2200 to 2700 feet away from the home area, homing success in natural areas is over twice that (33% as compared to 16%) of the golf course releases, even though many more animals were liberated in the course of the experiments at the latter. Of the 31 animals released on the golf course, only 2 were recaptured by the second night following release. The 3 other mice took considerably longer, and as noted 1 of these was retaken 2500 feet north of its homesite before it was recaptured in its home area. In natural

areas 2 of 6 mice released at 2200 to 2700 feet were recaptured, 1 by the second and the other by the third night following liberation. Considering that traps were available for recapture in the peripheral areas of the golf course for a much longer period of time than in natural areas and, as mentioned previously, it seems likely that the nature of the area surrounding the golf course might have to some extent directed the movements of the animals westward, which was in the direction of the home area, it strongly suggests that mice home with greater success in natural areas.

INITIAL ORIENTATION

From February to early September, 1959, observations were made on the initial movements of animals liberated at night on the golf course. Two groups of mice were used, a "local" series (also used for homing experiments) captured less than one mile from the release site and a "distant" series captured from four to 60 miles from the release area. The mice used in these experiments were captured in the morning and kept for 12 to 15 hours in the laboratory until the time of liberation at night. Several mice from the local sample were held in captivity up to 65 hours before release because of inclement weather, and 4 mice from 60 miles away were kept in the laboratory 13 days before release.

A step-ladder painted black for camouflage was used at the release site as an observation point. The experimental animal was transferred from a live trap to a bottomless hardward cloth cage measuring 5 inches x 3 inches x 3 inches and placed on the ground beneath the center of the ladder. After the mouse had been allowed a period of time for adjustment to its surroundings, the observer, seated on top of the ladder, gently raised the cage by means of an attached string.

A strip of cellophane tape with a 1 1/2 inch patch of luminous paint ("Lite Koat Mixture" manufactured by the General Cement Company, Rockford, Illinois) previously charged by a flashlight in a light-tight box was affixed to the dorsum of the mouse just before it was

transferred to the release cage. After liberation the mouse was observed directly or with the aid of a pair of 7 x 50 binoculars. The pattern of its movements was traced in as great detail as possible on data sheets which also included the date, time of night, location of homesite, temperature, wind direction and velocity, sky conditions, and other details. The animals were marked for permanent identification by toe-clipping.

The maximum distance any mouse was observed from the release point was approximately 175 feet and many of the mice required 12 to 13 minutes to move beyond the observer's range of vision.

Overcast or moonless nights provided best conditions for observations. The luminescent patch remained visible for approximately 15 minutes. The initial movements of mice in both groups were characteristically slow and usually very erratic. Randomly selected examples of initial movements from the two groups are shown in Figs. 7 and 8. In some instances the animals moved in spurts and occasionally followed a more or less circular pattern, sometimes returning to the release point several times. No correlation between speed of departure or the animal's initial course and the proximity or direction of the homesite was apparent under a variety of environmental conditions, including overcast and clear nights with and without a moon. However, clear moonlit nights tended to inhibit movements of the mice, which seemed hesitant to leave the area of shadow created by the observation post.

Further evidence that initial orientation movements on the first

Figure 7. Initial orientation patterns in unfamiliar territory of mice from the "local" population.

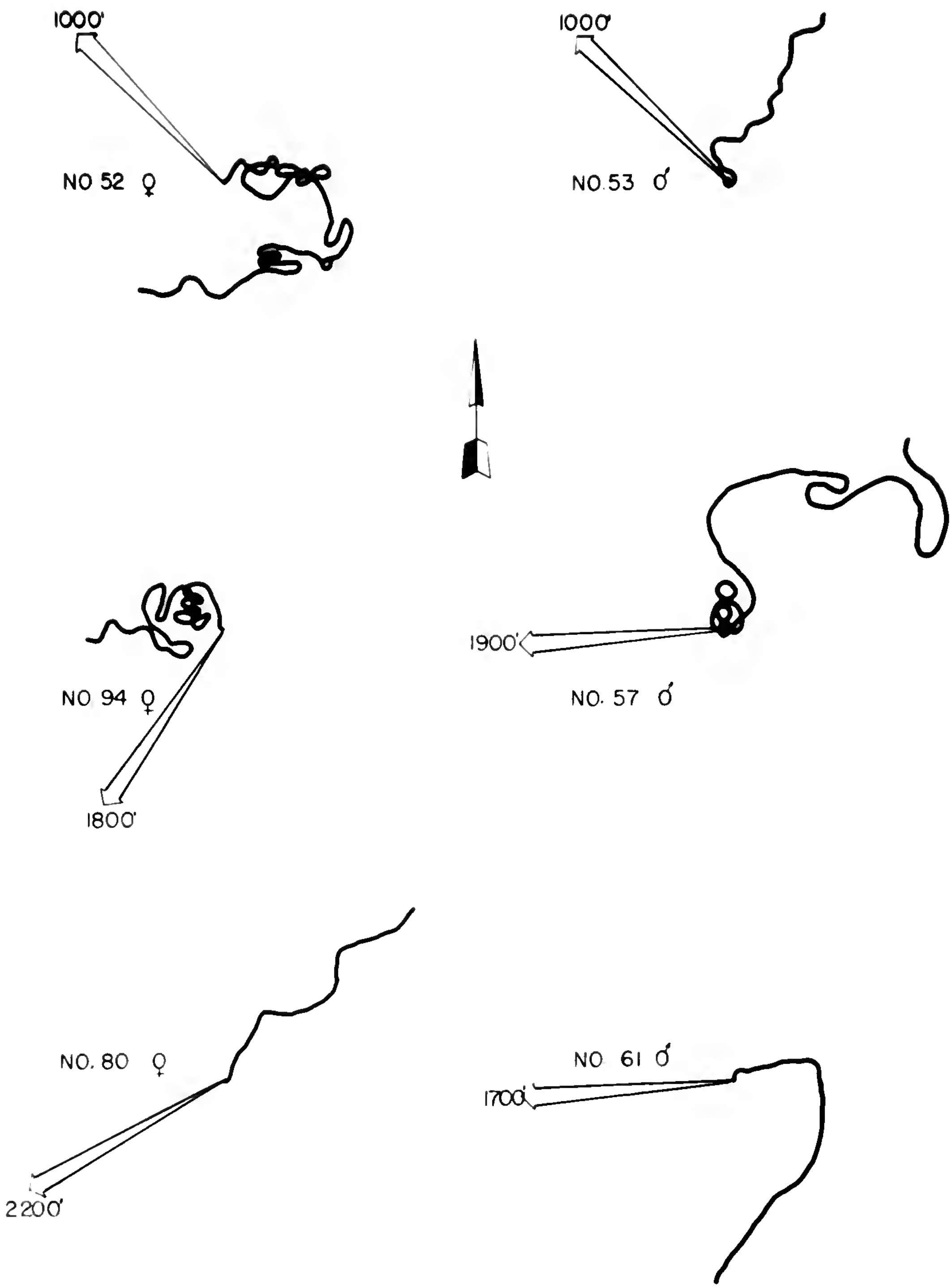


Figure 7

Figure 8. Initial orientation patterns in unfamiliar territory of mice from the "distant" populations.

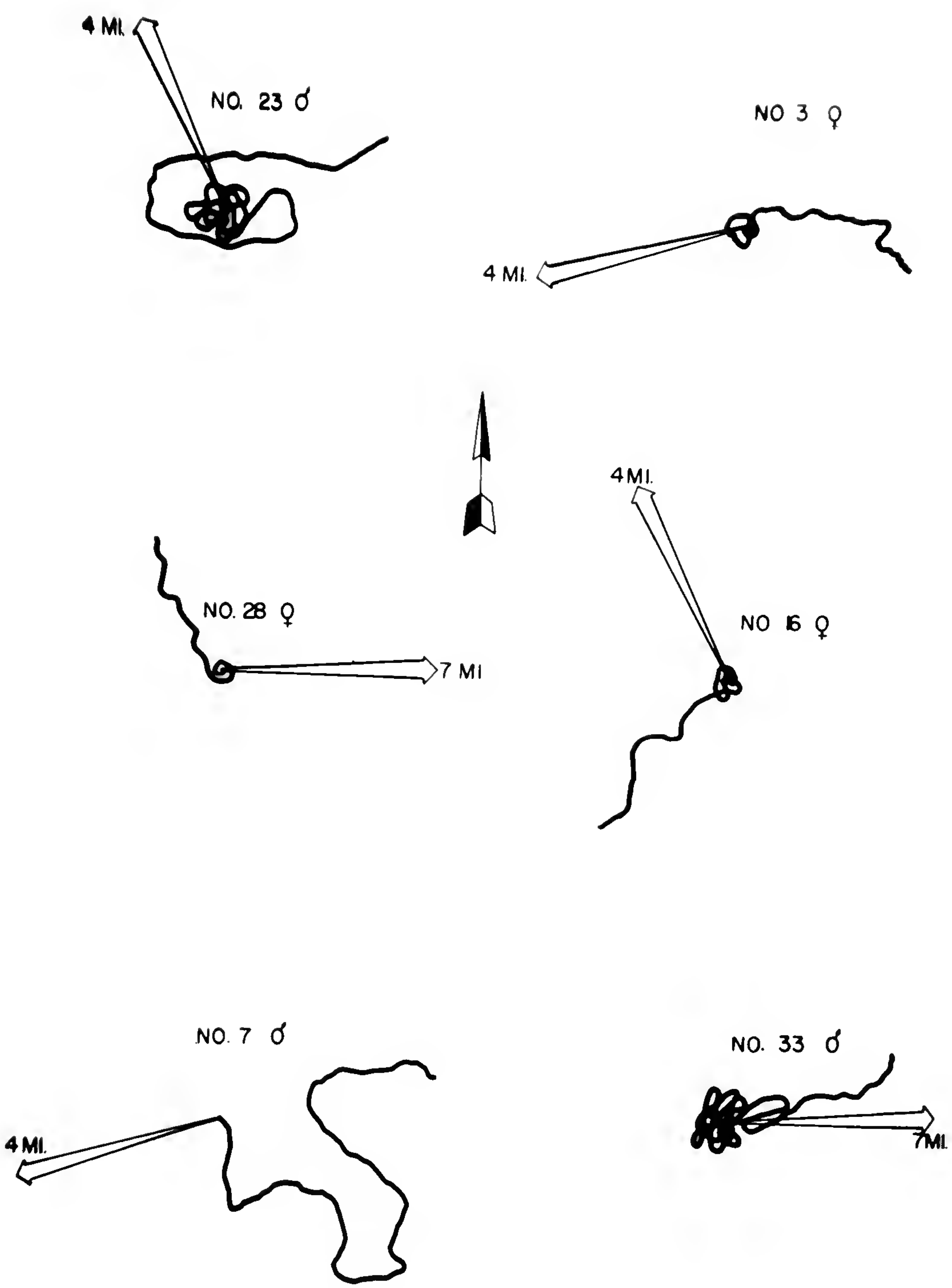


Figure 8

release were random with respect to the homesite is provided by an analysis of the selection of particular directional zones by mice when released. An imaginary line was drawn from the release point to the approximate homesite. Using the home bearing as the base line, the release area was divided into four equal zones. Zone +1 included the sector encompassed by a 45 degree angle on either side of the home bearing. Zone -1 included the opposite 90 degree sector, and the lateral zones were designated as O_1 and O_2.

Of 47 mice comprising the local sample, 10 (6 males, 4 females) selected Zone +1, 11 (8 males, 2 females, 1 juvenile) Zone O_1, 12 (8 males, 4 females) Zone O_2, and 14 (8 males, 6 females) Zone -1. In the case of the 42 mice constituting the distant sample, 9 (6 males, 3 females) selected Zone +1, 11 (7 males, 4 females) Zone O_1, 8 (4 males, 4 females) Zone O_2, and 14 (6 males, 8 females) Zone -1. The difference in these frequencies are not significant in either series on the basis of the chi-square test (local sample $X^2 = 0.95$, distant sample $X^2 = 1.98$).

The 15 animals from the local population that were subsequently recovered at their homesites had selected the following zones on their first release: Zone +1, 1 male released at 1800 feet and a female released at 1700 feet; Zone O_1, 1 male released at 1000 feet, 1 female released at 1800 feet and a male and female released at 2700 feet; Zone O_2, a male released at 1700 feet, 3 males released at 2700 feet and 2 females released at 1000 feet; and Zone -1, a male released at 1900 feet and 2 males released at 1000 feet. There is no

significant difference in the frequency of use of the four zones by these animals, indicating that even in the case of successfully homing mice there was no tendency to select the direction of the homesite when released for the first time in unfamiliar territory.

Seven of the 15 animals were regularly liberated and recaptured a number of times from the same release point. The observed movements at later releases were strikingly different from those of the first. In almost every test, the mouse moved rapidly and with little hesitation, often passing beyond the observation range within 30 seconds. During the course of these repetitive releases, it was noted that some mice appeared to utilize the same initial pattern of movement as on the first release, even though the pathway was unoriented with respect to the home direction. Such a tendency is indicated by mouse No. 51 whose initial orientation patterns are shown in Fig. 9. One animal, male No. 54, on its fifth release at a point 100 feet closer to the homesite than the usual distance (1000 feet) exhibited a pattern of movements similar to that of previous releases (Fig. 9). Another individual female, No. 52, was liberated 300 feet closer to the homesite on the fourth release than previously. Its path was oriented in the direction of the home area. It is possible that on this occasion the animal may have been responding to heavy shadows of the wooded section, which was much closer than usual due to the decreased release distance (Fig. 9).

Of the other successfully homing animals from this group, 3 were not again used in this or other experiments. Five were subsequently

Figure 9. Initial orientation patterns of 6 mice released repetitively at the same point on the golf course.

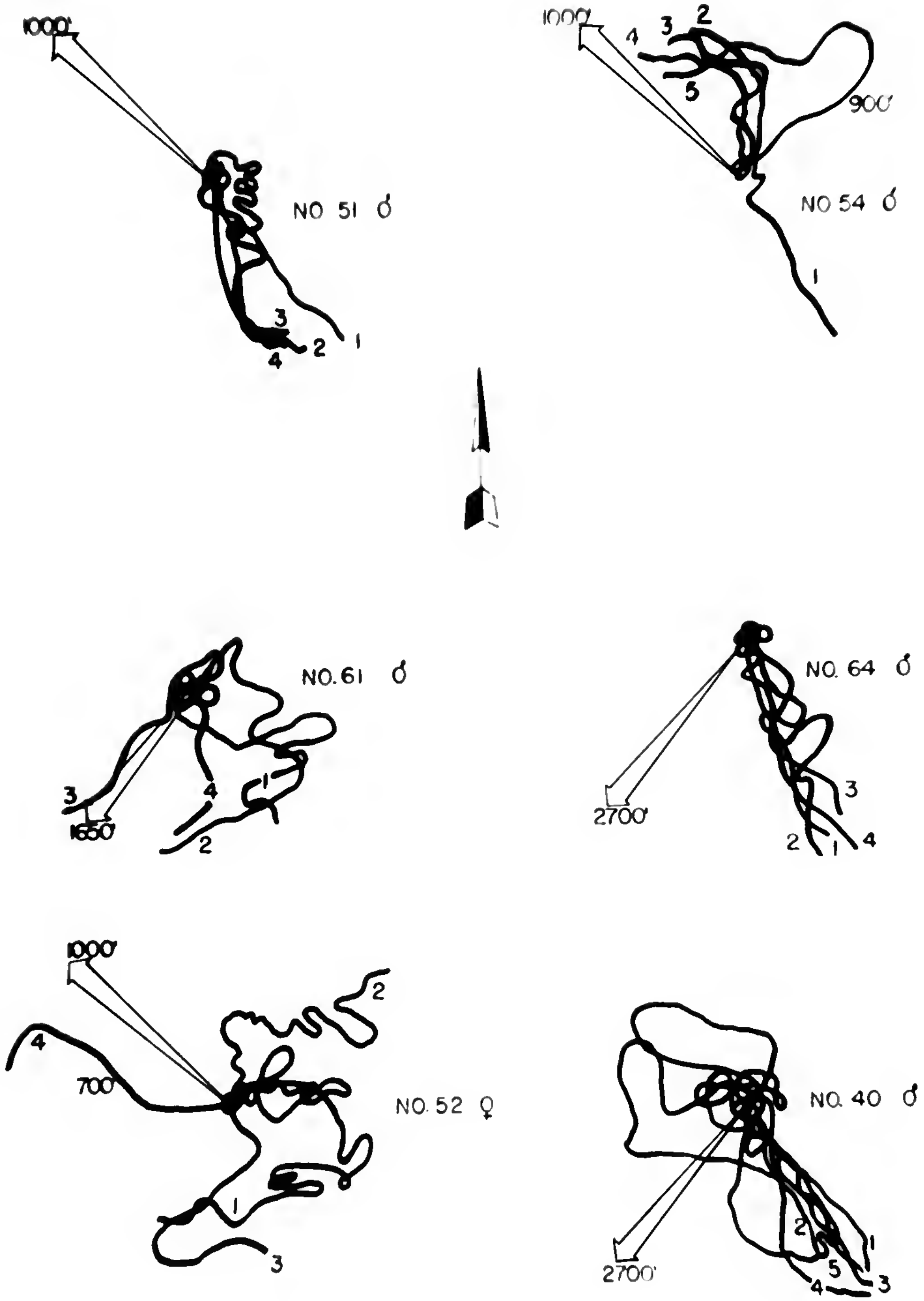

1000'
NO 51 ♂
1000'
900'
NO 54 ♂
NO.61 ♂
1650'
NO. 64 ♂
2700'
1000'
700'
NO. 52 ♀
NO. 40 ♂
2700'

Figure 9

released a total of 15 times at different points on the golf course varying from approximately 1000 to 2200 feet from their capture sites, and in general their initial movements were more rapid than on the first release. One animal was not recovered after its second release. The remaining 4 returned to their homesites in from one to three nights on several later occasions, which suggests that they may have acquired a familiarity with a considerable portion of the golf course as a result of previous releases.

Eleven of the 42 mice (26 %) from "distant" populations were recovered at the peripheral areas of the golf course in the interval of about four months after the initial liberation. Six of the 11 were released a second time at points different from the original ones. The distances ranged from approximately 1000 to 2000 feet from the last capture site. In general, these animals moved rather rapidly upon liberation though none of them was recovered again. The other 5 mice were released a second time at the original points, and their movements were also noticeably more direct. Four of these were recaptured again and released at other points on the golf course. In all, these mice were retaken on 17 occasions at different places and at intervals ranging from two days to four months between release and recapture. This suggests that the animals were wandering and had not established definite home ranges. The fifth animal was liberated a total of seven times at the same release point. Although its pattern of initial movements seemed to change with each release, this mouse, female No. 25, from a "distant" population (60 miles) consistently

returned to the same trap in the northwest corner of the golf course on the same night that it was liberated (Fig. 5). On its third release at 1000 feet the animal was retaken in the usual trap within three hours after liberation. This suggests that some cotton mice that do not locate their former home ranges may settle quickly in a new area. Burt (1940), Murie and Murie (1931), and Stickel (1949) have noted a similar tendency for certain mice to remain in the vicinity of the release site.

Briefly stated, the results of the initial orientation experiments suggest that mice released in completely strange territory, whether near or distant from the home area, move in a random fashion from the release point with respect to the homesite. Animals that are successful in finding their home area and are released again at the original point may return by the previous pathway, although indirect. Their movements in subsequent trials, however, are more rapid because they are not traveling over familiar territory. Mice from distant sources which establish home ranges in the new region behave as do local animals on subsequent releases.

It is difficult to say exactly what cues animals use for orientation under these circumstances. Vision probably plays an important role, although other sense modalities may also be involved to a significant degree.

RETENTION EXPERIMENTS

During the summer of 1959 several experiments designed to provide some indication of the degree of attachment for the home area and the role of learning and memory in homing behavior were conducted. Mice of varying previous homing experience were removed from the San Felasco and Ft. Clark study populations and retained in the laboratory for periods of time ranging from 32 to 87 days. During the period of retention the mice were kept in a small animal room which housed several other species of mammals. The mice were kept in small cages with two individuals of the same sex per cage. Food and water were provided *ad libitum* and nesting material was supplied. After the retention period, the animals were returned to the study areas where they were liberated just prior to sundown. Some were released at different distances from the home area, while others were replaced within their former home ranges. Trapping was conducted for various periods of time afterwards to obtain data on the subsequent movements of the released animals.

The first experiment involved 12 animals (7 males, 5 females). Eight of these had been used in homing experiments at San Felasco and, therefore, were presumed to be familiar with some of the area immediately outside their trap-revealed home ranges. After laboratory isolation of from 34 to 35 days, a control group of 6 mice (2 males, 4 females) was liberated within the former home ranges of the

individuals. Three females in this group had been used in homing experiments previously. Of the remaining 6 animals (5 males, 1 female) 5 were released at points that the individuals had presumably traversed in the original homing experiments. These releases included 1 male at 450 feet, 1 male and 1 female at 500 feet, and 2 males at 900 feet. A male in this group that had not been used in the original homing experiments was released at 700 feet. The distances given in each case were measured from the limits of the known home ranges to the release point. Traps were set on the grid prior to release and the area was trapped for five consecutive nights. Of the animals liberated in their former home ranges all were retrapped, the 6 mice being retaken a total of 12 times during the first trapping period. None of these individuals was taken in traps beyond the boundaries of the previously calculated home range. Only one animal was taken the first night of trapping. Five of the 6 mice liberated in their former home ranges at distances ranging from 450 to 900 feet were retaken 11 times during the trapping period. One was retaken on the night of liberation 300 feet outside its home range but when retrapped the next night was within its former home area. All of the others were taken only within the calculated boundaries of their home ranges. The one animal not recaptured was a female liberated at 500 feet; it had successfully homed from the same distance in the original homing experiments.

Trapping in the area about six weeks later revealed that 7 of the 11 mice that were used in the retention experiment (the other 4 of the

original group had been removed to the laboratory for another experiment) were persisting in their original home ranges. These 7 animals were retaken 18 times during six nights of trapping, the recaptures of each being restricted to the previously calculated home range.

A second experiment was performed using 14 animals (7 males, 7 females) that were held in captivity for 32 to 34 days. One male was released within its former home range. The other animals were released outside their former home ranges as follows: 1 male and 2 females at 300 feet, 1 female and 2 males at 400 feet, 1 male at 500 feet, 1 female at 550 feet, 1 male at 650 feet, 1 male and 2 females at 700 feet, and 1 female at 900 feet. Four of the animals tested had been used in the previous experiment and therefore had been retained in the laboratory for more than 60 days with an interruption of five nights during the first experiment. Of the remaining 10 animals, 8 had never been used in any other phase of the study. Trapping was conducted for six consecutive nights beginning with the second night following liberation.

Thirteen of the 14 animals released were re-trapped a total of 40 times. On the first night that traps were available, 2 mice were retaken outside their home ranges, although both animals were later (second and fourth nights) recovered in their respective home areas. All other mice were never recaptured outside of their original home ranges. Only 1 animal, a male liberated at 500 feet, was not retaken. This animal had not been used in any of the previous experiments and had a home range at the periphery of the study area which

might have extended beyond the plot. Consequently, it probably had a lower probability of capture and might have returned without being recovered.

In some cases, observations were made on the initial movements of the animals at the time of liberation. On one occasion, 2 mice were released simultaneously at the same site. One of the individuals was known to have previously nested in a particular log about 10 feet from the release point, while the other mouse was 500 feet outside its former home range. The activities of the 2 mice were distinctly different, the one formerly occupying the area moved rapidly to a small hole in the log after a few seconds of hesitation, while the other mouse moved more slowly, lingering within a few feet of the observer and appeared to be examining various objects. The latter mouse was observed for about ten minutes and was eventually lost in some fallen trees 30 feet from the release point and in the general direction of its former home area.

One mouse released in its former home range moved with very little hesitation and on a direct course to a tree root 35 to 40 feet away that had been occupied during the home range studies some 15 to 16 weeks before. Another mouse released in its former home range moved a short distance away from me then turned and ran rapidly between my legs to a slight depression in the ground five feet from where it was liberated. The depression was completely covered with ground litter and did not appear to be a regular homesite. Closer examination revealed a small hole in a log buried beneath the litter. The mouse had

apparently entered this hole, and its actions left the distinct impression that it had intentionally sought this refuge. The other animals liberated in this experiment were out of sight soon after release, and observations on their movements could not be made accurately.

Two more retention experiments were performed with 3 animals at Ft. Clark. The periods of isolation were 38 and 87 days. The trapping plan, as already indicated, consisted of ten stations on either side of a sand road. Two males were used in the first experiment, 1 of the 2 having first been conditioned to homing from 950 feet and the other from 1200 feet. After 38 days of laboratory isolation, the individual conditioned to 950 feet was released at 700 feet. It was not recovered during subsequent trapping. The other male was liberated at 500 feet at a point making it necessary for it to encounter several trapping stations if it were to use the first direct route in returning home. This animal was recovered at its original homesite on the second night following release. After its first return, liberations were made at 1000, 1500, 2000, and 2500 feet. Several of these releases were in a direction that made it necessary for the mouse to encounter four trapping stations if it were to use the direct route in returning. In each case the animal was recovered at its homesite on the same night it was liberated.

This successfully homing male was again removed to the laboratory and isolated for an additional 87 days. A female conditioned to homing from 1150 feet was also retained for the same length of time.

After the isolation period, both animals were released at 1000 feet on the opposite side of the road from which they were originally taken, making it necessary for the mice to cross the road if they were to regain their homesites. On the second night of trapping, both mice were recovered at the exact station where they had been caught previous to the period of isolation. Liberations at 1500 feet were then made, and both mice were back the same night. Further releases were not made, but during two nights of additional trapping, the male was retaken twice and the female once, indicating that they were persisting at their respective homesites. It is of interest to note that during the 87-day period the mice were kept in captivity the vegetational aspect of the study plot had changed markedly. A five to ten foot wide strip of vegetation bordering the road had grown to approximately five to six feet from an initial height of about one foot, and the foliage had grown considerably denser.

The retention experiments seem to clearly indicate that the cotton mouse is able to recognize its former home range and retains a strong motivation to return to it even after a rather prolonged absence. The mice also appear capable of remembering for an equally long period of time terrain infrequently traversed and outside the normal limits of the home range.

DISCUSSION

Homing results obtained in the present study suggest, as do those for other small mammals, that cotton mice have a strong attachment to their current home range and are strongly motivated to return to this area when removed from it. The apparent lack of response to available traps outside the calculated home range observed in many instances may also be taken to indicate that a mouse responds differently to objects in the environment inside and outside of a familiar zone, which argues further that the familiar zone has a unique significance for the individual. Data from the retention experiments suggest that the memory of the home range and motivation to return to it are remarkably persistent when considered in relation to the average ecological longevity of six months reported by McCarley (1959) for the species in Texas.

The foregoing considerations appear to have implications in connection with our present concept of the home range of small mammals. Most attention given to the significance of the home range has emphasized the somatic aspects. That is, the home range is the area over which an animal travels in obtaining food, homesites, mates, etc., and with which it is intimately familiar and thus better able to find cover when escaping from enemies. It may be assumed that the home range not only satisfies the animal's physical needs, which might often be provided for equally well or better in other areas, but has

some psychic significance. In other words, the home range offers a wide variety of associations with environmental objects to which the animal is intimately attached. Within this familiar area, the animal moves with assurance. If displaced artificially from its home area the animal may become psychologically disturbed. This state may also be accompanied by physiological changes similar to those symptomatic of stress, resulting in a search for familiar territory.

Although field-data to support this hypothesis are apparently nonexistent, laboratory experiments performed by Southwick (1959) appear to have a bearing on the question. In this experiment, young adult mice (*Mus musculus*, brown strain) were subjected to three different types of short term behavioral disturbance for one hour a day, and direct eosinophil counts were taken four hours later. Speirs and Meyer (1949) have shown that a stress of short duration produces a temporary eosinopenia in which the eosinophil count reaches its lowest level about four hours after the onset of stress. Thus the number of circulating eosinophils at this time may be considered to be an index of the degree of systemic stress.

Southwick's results showed that placing isolated males in groups of four in large cages for one hour and then returning them to their original cages resulted in an 80 percent decline in circulating eosinophils for each of eight days of experimental trials. Males that were held for one hour in cages previously occupied by another male mouse and then replaced in their own cages showed a 75 percent decline in eosinophils for two days but the counts gradually returned to normal

by the eighth day. Mice that were gently handled for a few seconds at the beginning and end of an hour and returned to their own cages did not exhibit a significant change in eosinophil levels. The results indicate that the mere transferring of an animal to a new, but physically similar environment constitutes a relatively stressful experience. It is possible that under natural conditions wild rodents removed from the home area may show a similar response, even though the habitat in which they are released is physically similar to that of the home area. The accompanying psychological unrest may then stimulate them to look for their home areas.

Granted that small mammals have a "home sense" and are strongly motivated to return to their established home area, the question of the means by which this is accomplished must be considered. Celestial cues, including polarization patterns in the sky, the sun, stars, and moon, have been implicated in the orientation of several rather widely separated and diversified groups of animals (Carthy, 1956; Sauer, 1958). No evidence obtained in this study indicated that celestial bodies were used directly by mice in homing from the distances used, although such factors as shadows created by moonlight influenced to a certain extent the patterns and rates of at least initial movements after release. Rawson (1956) has indicated that mice successfully home under overcast skies from relatively short distances, and Bovet (personal communication), on the basis of preliminary experiments, has tentatively concluded that red mice (Evotomys = Clethrionomys) and wood mice (Apodemus) do not utilize the sun in homing.

On the basis of the evidence gathered in this investigation, it is postulated that homing was accomplished in two ways: 1) random wandering in unfamiliar terrain until and if a familiar area is encountered, and 2) nonrandom movements in terrain with which the animal had some previous familiarity.

The first explanation appears to apply to the golf course experiments in which initial orientation of mice released for the first time was apparently random. In addition, the time required for recapture in homing tests was appreciably higher than in natural areas, and the proportion of recaptures from the greater distances was lower. The idea of random wandering is further supported by the observations on 4 mice whose recaptures during the several days following release suggested that the animals were unoriented with respect to a direct homing route. Animals which by chance select a pathway in the direction of their homesites may return in a short interval over a relatively long distance. Such returns may be aided by a directing influence of certain environmental features such as roads, waterways, open fields, and topographic irregularities.

Much of the homing recorded in this study is believed to have been a nonrandom activity with respect to the homesite. In other words, the animals had in actuality not been released in completely unfamiliar terrain. This view supposes that the mice are familiar to a certain extent with an area considerably larger than the calculated home range. There are several ways in which this broader knowledge of the environment may be gained. These include actually larger home

ranges than are revealed by conventional methods, occasional exploratory sallies outside the home range, shifting of home ranges, and dispersal from the birthplace.

Chitty (1937) and others have suggested that small rodents may have larger home ranges than can be determined by standard trapping techniques. Such procedures as are presently employed in studying small mammal home ranges may merely give an index of the area an animal regularly encompases in seeking its requirements. The various techniques of home range determination and the relationship between "trap-revealed" and "true" home ranges have been considered by Hayne (1949, 1950), and Stickel (1954).

Occasional trips beyond the usual home range would permit "exploratory learning" (Thorpe, 1956) and actually represent instances of "natural" homing. Such movements have been recognized in various small mammals (e.g., Blair, 1940, 1943; Storer, Evans, and Palmer, 1944). Small mammals are also known to shift the home range from one period to another or expand or contract its limits (e.g., Burt, 1940; Blair, 1940) and in this manner probably become familiar with additional terrain.

Dispersal from the birthplace may be a rather important way in which rodents obtain a knowledge of a larger general area than ordinarily encompassed by the home range. In this connection, an analysis of dispersal and homing data obtained for *Peromyscus leucopus* and *P. maniculatus* by Burt (1940), Howard (1949), Stickel (1949), Dice and Howard (1951), and Murie and Murie (1931, 1932) supports the conclusion

that at least a part of homing success of small mammals can be attributed to familiarity with terrain acquired during dispersal. A graphic illustration of these data is presented in Fig. 10. It will be noted that for the two species concerned there is a close correlation between dispersal distance and homing success. The tendency for recapture of fewer animals liberated at the greater distances in homing experiments therefore seems to be related, among other things, to the dispersal of the species. Thus, the greater the distance an animal is released from the homesite the less the chance it has had previous experience in the terrain and the lower its probability of return. Records such as the one reported by Murie and Murie (1931) in which 1 of 23 animals released at two miles was recovered at its homesite in only 48 hours after liberation suggest that the animal may have had a prior knowledge of the area gained, perhaps, during dispersal. Schieldt (1951) recovered 2 mice in 10 to 15 minutes after releasing them at 1000 feet.

Much evidence points to the fact that in small mammals, males have a wider range of activity than females. In considering the sex differences in dispersal, the data of Burt (1940), Howard (1949), and Dice and Howard (1951) are graphically illustrated in Fig. 11. The chi-square values in each case represent adjusted values whether or not the sample was a small one. In general, these data show that short distance dispersal from the birthplace occurs with approximately equal frequency in males and females and the differences are not statistically significant. Dispersal to the greater distances is,

Figure 10. Comparison of homing success and dispersal distance of two species of *Peromyscus*.

Figure 11. Comparison of sex differences in homing success and dispersal distance of two species of *Peromyscus*.

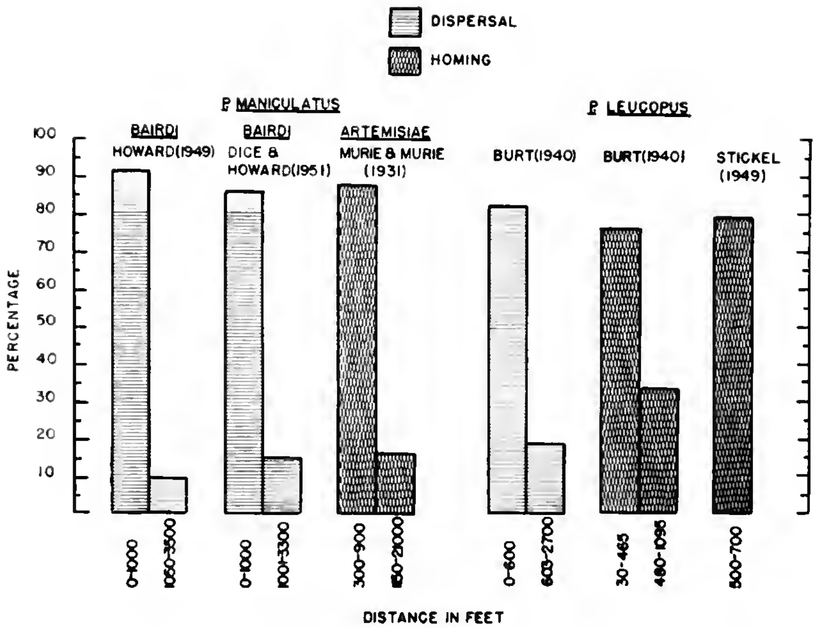


Figure 10

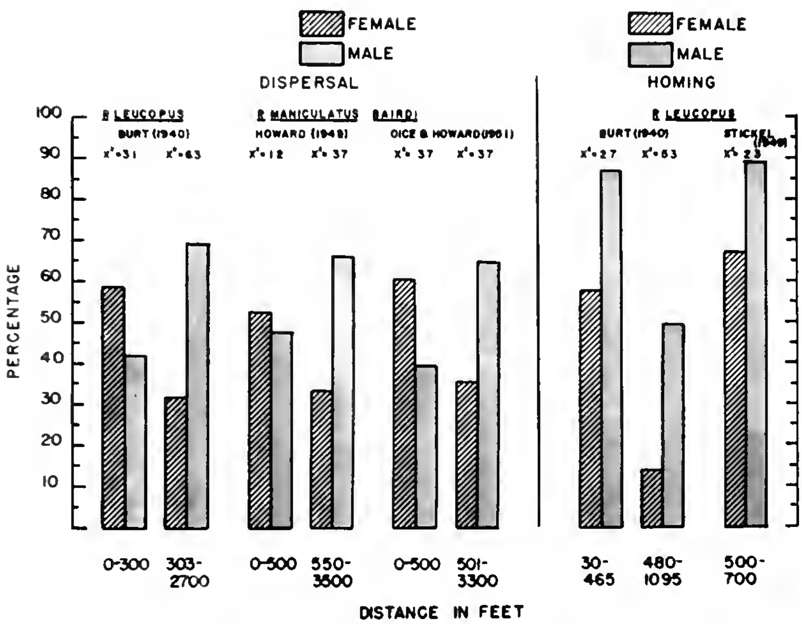


Figure 11

however, more frequent in males and the difference is statistically significant in the case of Burt's data. The homing success of males and females of P. leucopus (Burt, 1940, and personal communication; Stickel, 1949) exhibits a close correlation with dispersal distance (Fig. 11). A sex difference in home range size with males averaging larger home ranges than females is indicated in this study and a similar trend has been reported for other species of small mammals. Barrington (1949), Pournelle (1950), and Pearson (1953) each reported a more extensive wandering habit in males of P. gossypinus. This evidence further suggests that males tend to be familiar with a greater area than females. If the suggestion that much of homing success in small mammals is the result of familiarity with the terrain surrounding the home area is correct, then one would expect to obtain higher homing success in males than females at least at the greater distances. On the basis of this hypothesis, no difference in homing success of males and females released in totally unfamiliar territory would be expected. Such does appear to be the case in the golf course experiments where nearly the same proportion of males and females, 33 and 31 percent, respectively, returned from first releases. These results seem to indicate random wandering in unfamiliar territory.

The question now arises, are animals capable of learning the features of the terrain and homing pathways at an early age, and if they can, whether or not they can retain a memory of such familiarity for a prolonged period of time? Feniuk and Popova (1940) in their homing experiments with rodents concluded that young mice (juveniles)

that have not become independent of their nests do not show homing ability. The explanation of this may be two-fold. First they may lack the motivation needed for homing and second they may lack the familiarity with the terrain around their birthplaces.

This suggests that the dispersal and establishment of an adult home range are generally important for homing ability. Although the evidence is admittedly circumstantial, the fact that the same initial pathway was often followed in subsequent releases of successfully homing animals on the golf course and that movements were more rapid suggests that an animal need traverse an area one time whereupon the homing pathway is familiar and apparently learned. This is evident in the recaptures of 11 of the 12 successfully homing animals when released more than one time on the golf course and the return of several within a matter of hours. In this connection, Harrison (1958) concluded that *Rattus* was able to learn homing routes and that subsequent release of successfully homing animals at the same point of liberation results in a much higher percentage of returns. A similar trend can be found in the work of Murie and Murie (1931), Rawson (1956), and Feniuk and Popova (1940), each of whom recorded higher homing returns from subsequent releases of successfully homing mice. The contention that learning and memory do play a role in homing ability is further supported by the retention experiments, in which mice seemed to recognize their home ranges and were remarkably successful in homing with or without experimental experience prior to laboratory isolation. It seems possible, therefore, that cotton mice

learn and retain for extended periods of time a memory of the terrain encountered during dispersal and subsequently use this familiarity in homing.

The results reported in this paper by no means identify the particular sensory mechanisms utilized in homing. Visual cues may be important. Bodenheimer and Kornhauser (1955) have shown that wild mice have the ability to discern visual differences and to utilize them in learning a situation. However, other sense modalities such as auditory and chemical senses probably also play a role. It appears likely that by utilizing the ordinary senses mice are capable of learning and retaining for prolonged periods of time a schema of their near and more distant environments and to utilize this familiarity in homing activity.

Further, it seems appropriate to suggest that psychic factors are important in a consideration of home range and homing. Based on the degree of psychological attachment to an area, small rodents may be considered to have three types of zones: 1) Territory, as defined by Burt (1943), which is the protected part of the home range; 2) Home Range, or a zone of intimate familiarity and close affinity; and 3) Life Range, or a zone of general familiarity gained as a result of dispersal, occasional wandering, and home range shifts. Homing from within the life range is assumed to be a nonrandom activity with respect to the homesites, whereas homing from beyond the life range, hence from totally unfamiliar territory, is probably by means of random wandering until familiar terrain is encountered.

SUMMARY AND CONCLUSIONS

A study of homing in the cotton mouse, *Peromyscus gossypinus*, was conducted at four localities in northcentral Florida from February to September, 1959. Approximately 175 animals were utilized.

Based on a grid trapping plan and the inclusive boundary strip method of analysis, the mean home range of 25 mice was 1.57 ± .17 acres. Males averaged larger home ranges than females.

In homing experiments in natural areas, 54 mice (27 males, 27 females) were liberated away from home for the first time at distances ranging from 100 to 2500 feet. Of this number, 44 mice (81 %) were recovered including 85 percent of the males (23) and 78 percent of the females (21). All individuals of both sexes were retaken from 500 feet while only 78 percent of the males and 60 percent of the females homed from distances ranging from 600 to 2500 feet.

In 101 multiple releases of successfully homing animals in natural areas at distances ranging from 100 to 2500 feet, 84 recoveries (83 %) were made. This included 86 percent of the male releases and 80 percent of the female releases. Of the releases ranging from 100 to 500 feet, all of the males (17) and 92 percent of the females (25 of 27) were recovered. In the displacements ranging from 550 to 2500 feet, 79 percent of the males (27) and 65 percent of the females (15) were retaken.

Homing success of animals released in an unnatural habitat (golf

course) adjacent to their home area was less than that in natural areas at comparable distances. Forty-seven mice were liberated at 1000 to 2700 feet and 15 (32 %) were recovered including 33 percent of the adult males and 31 percent of the adult females. These required a substantially longer period of time for recapture when compared to data for releases at corresponding distances in natural areas.

Initial orientation observed under nighttime conditions in unnatural habitat appeared to be random with respect to the homesite and celestial bodies seemed to have had no directing effect on their initial movements in relation to the location of their habitation.

Repetitive liberations of successfully homing mice from the same release site on the golf course indicated that a single successful homing experience usually results in more rapid returns on subsequent releases from the same point and that the initial pathway continues to be utilized during subsequent releases.

In retention experiments mice which had homed a number of times and were then held in laboratory captivity for periods of more than 12 weeks before being liberated at former release sites showed no decline in their homing performance.

Animals released in their former home ranges occupied prior to extended periods of laboratory isolation (32 to 35 days) remained and maintained these areas.

A number of animals without previous experience from artificial displacement returned to and maintained their former home ranges when released at various distances from their capture sites after prolonged

periods (32 to 35 days) of laboratory isolation.

The results indicate that cotton mice are capable of learning and retaining for prolonged periods of time a schema of their environment and are able to utilize this familiarity in homing activity.

It is postulated that psychological factors are the principal source of the motivation to home. Based on the degree of psychological attachment to an area small rodents may have three types of zones: 1) Territory; 2) Home range; and 3) Life Range. The latter is considered to be all the area an animal traverses during its life cycle.

The present data are interpreted to indicate that the mechanism of homing in P. gossypinus involves random movements outside the life range with respect to the homesite and directed movements in relation to the home area from within the life range. In the latter case the animal utilizes a previous familiarity with the general area gained by occasional exploratory wandering, home range shifting, and dispersal from the birthplace.

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BIOGRAPHICAL SKETCH

James Vincent Griffo, Jr., was born at Brooklyn, New York, on September 17, 1928. He received his elementary and secondary education in the public schools of Kings County, New York. Undergraduate study in zoology was taken at Sampson, Champlain, and Brooklyn Colleges. In September, 1950, he transferred to the University of Kentucky where he completed the requirements for the Bachelor of Science in January, 1952. He then enrolled in the Graduate School at the same institution, majoring in parasitology and public health, and received the Master of Science in June, 1953. He served as a medical parasitologist in the United States Army from November, 1953, to December, 1955. Upon discharge he enrolled at the University of Tennessee where he was employed as a research assistant in parasitology until May, 1956. In June, 1956, he transferred to the University of Florida to continue study for the doctorate in the Department of Biology. He has served as a graduate, research, and teaching assistant. He is married and has two children. He is a member of Sigma Xi, Phi Sigma, The American Society of Mammalogists, The Ecological Society of America, The American Society of Parasitology, The Wildlife Society, and the Entomological Society of America.

This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

June 6, 1960

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